(138)
1968

EXPERIMENTAL NEUROLOGY 21, 92–104 (1968)

Bimanual Coordination in Monk[illegible]

R. F. MARK AND R. W. SPERR[illegible]
Division of Biology, California Institute of T[illegible]
Pasadena, California 91109

Received February 28, 1968

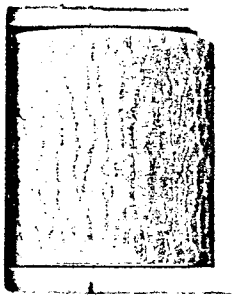
In respect to their agility and muscular coordination, monkeys in which the corpus callosum has been sectioned are hardly distinguishable from normal animals. Nevertheless, certain movement patterns involving the use of both hands might be expected to depend on direct connections between the hemispheres since the main cortical motor centers for each hand lie in opposite hemispheres. In these experiments a behavioral test was used to measure the proficiency in aim and timing of hand movements where the sensory information for direction, distance, and timing of the target came from proprioceptive and kinesthetic cues originating in the other arm. Testing of monkeys with various midline brain lesions showed that section of either the corpus callosum or tectal cross-connections alone produced only a transient loss of skill in the task. If forebrain and midbrain commissures were both severed, however, a long-lasting deficit became apparent when the task was attempted without vision. With visual guidance of hand movement, performance remained essentially normal. With continued postoperative practice over several months the accuracy of spatial coordination of hand movements slowly improved until even when working blind, performance scores were once again normal and further were unaffected by an almost complete midline division of the cerebellum.

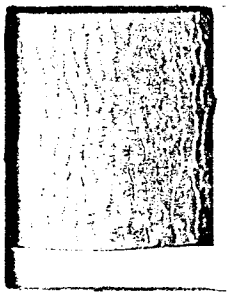
Introduction

Section of forebrain commissures disjoins the main cortical centers for right and left hands and for the right and left halves of the visual field thereby creating problems for right-left cross integration in a variety of visual, somesthetic, and related intermodal and sensory-manual functions. Among other circuits seemingly disrupted are those for the voluntary control of hand movement where the hand is guided by sensory information projected only to the wrong hemisphere.

Guidance of the hand by vision under the foregoing conditions has been studied in some detail. Control of the ipsilateral or disfavored hand has been shown to be remarkably preserved in cat (20), monkey (9, 18), and even in man (7, 23). Definite defects nevertheless can be demonstrated

[1] Aided by USPHS grant MH3372. The authors thank Lois MacBird and Ruth Johnson for their technical assistance. Dr. Mark's present address is: Physiology Department, Monash University, Clayton, Victoria, Australia.





under particular conditions and these conditions are becoming increasingly clarified as the observations and testing methods become more refined (3, 5, 7, 19, 23, 24).

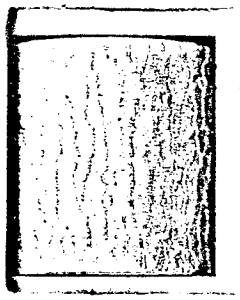
Much less attention has been given to the same problem in the somesthetic sphere that arises whenever a split-brain mammal needs to guide a hand or paw with reference to stimuli received only through the opposite hand. This is a common occurrence in bimanual activities that involve cooperative bilateral stereognosis. Again, the cortical areas receiving the sensory inflow are cut off by commissurotomy from the main motor control in the opposite hemisphere. The expected disruption of intermanual coordination under these conditions can be demonstrated after commissurotomy in human subjects (7, 21-23). In subhuman forms, however, the moment-to-moment integration of right and left limbs has seemed so far to be remarkably unimpaired even after commissurotomies extending deep into the midbrain (4, 25).

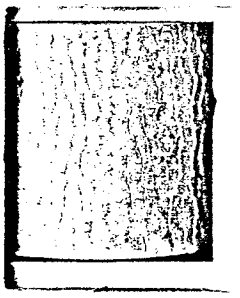
An attempt was made in the present experiment to study the somesthetic problem more specifically by training monkeys to aim one hand at a target (a free-falling peanut) under conditions in which the sensory information for the direction, distance, and timing of the target came from proprioceptive and kinesthetic cues originating in the other arm. Various animals in which the corpus collosum and other cerebral cross connections were sectioned progressively have been tested in an effort to learn more about the nature of the cerebral mechanisms involved.

Methods

Six monkeys were used for these experiments. Three adult pigtails (*Macaca nemestrina*), one *Macaca cynamolgus,* and two stump-tailed *Macaca speciosa.*

Training Procedures. The animals were first placed in an open cage and taught to obtain a reward from a dispenser mounted on a stick held in the experimenter's hand. The dispenser held a single peanut lodged in the middle of a narrow vertical tube against a rubber strip partially blocking the lumen. The peanut could only be released by pushing it past the obstruction with the finger of one hand and collecting it with the other hand at the lower end of the tube. The animals were then trained to operate a similar device inserted into a hole in a Plexiglas sheet. The hand collecting the peanut at the lower exit of the tube was placed below the sheet, while the other hand freed the peanut from above. When this was mastered, each animal was transferred for testing sessions into a special testing unit in which vision could be controlled by opening or closing eye slots (Fig. 1). The peanut dispenser was presented on a horizontal, perforated Plexiglas board which was mounted upon a carriage that moved





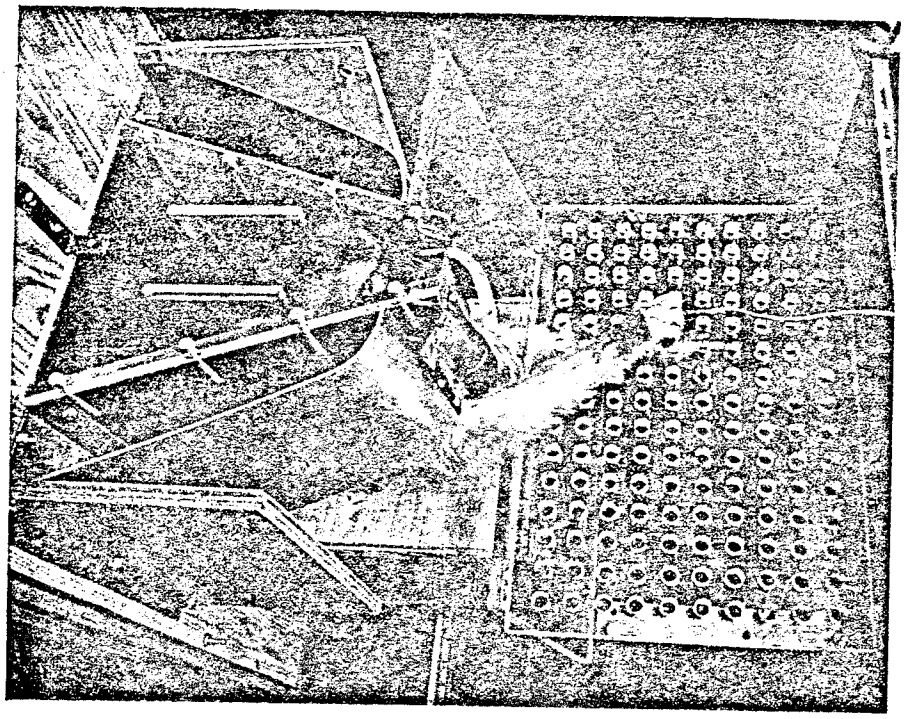


FIG. 1. Photograph of the apparatus for testing bimanual co-ordination in monkeys. A description is provided in the text.

smoothly on rails placed in front of the training unit. The perforations formed a rectangular grid of holes spaced 1 inch apart on the board, and thus for each trial the dispenser could be located at a different position relative to the animal. It projected about 1 cm above the board, and could be found from above either by vision or by touch. It did not project below the board so the animal could not tell by feeling from below from which hole the peanut would fall when it was released from above. The Plexiglas board also kept the two hands apart with no way for one to locate the other by direct touch. The proportion of rewards collected therefore gave a roughly quantitative measure of the ability of the animals to coordinate their two hands in space and time without any direct intermanual contact. Any peanuts not caught by the lower hand fell out of the animal's reach so that only successful trials were rewarded. Once the task could be performed under direct vision, the eye slots were progressively closed until the animals were orking blind. Five of the six animals were taught to operate the dispenser with either hand and to catch the reward with the

opposite hand. The remaining animal could only operate the dispenser with the left hand and catch with the right hand.

Testing Procedures. The animal's reach with each hand was first mapped on the board and then at subsequent sessions the peanut dispenser was placed in holes within the periphery of the mapped area, in a randomized order. In all but one animal both hand combinations were tested with the eye slots opened and closed. All four combinations were examined in the majority of the testing sessions. About 80–100 trials were run each day. The animal's performance was scored on a map of the board and a chart was kept showing the percentage of successful trials under each of the testing conditions (e.g., Figs. 2–6).

Surgical and Anatomical Procedures. Operations were done under general anesthesia following regular procedures for cerebral commissurotomy (21, 22). After craniotomy, the exposed hemispheres were retracted until the structures to be divided were visualized through a dissecting microscope. The sections were made by gentle suction, blood vessels being spared whenever possible. The bone plate was hinged loosely to allow for the severe cerebral swelling that characteristically reaches a peak about day 4 following such surgery. At the end of the experiment, the animals were anesthetized and perfused with 10% formalin. The brains were removed, serial frozen sections were made and stained by Weil's method for myelin sheaths. All the lesions illustrated are based on histological reconstructions.

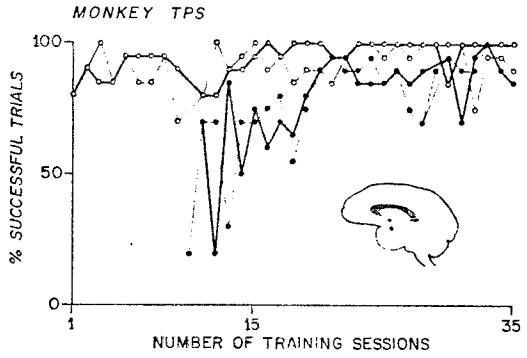


FIG. 2. Co-ordination scores of monkey TPS after preliminary training. Ordinate: percentage of successful trials under each of the testing conditions. Abscissa: number of training sessions. Open circles: eye-slots open. Filled circles: eye slots closed. Thick lines: right hand above board, left hand collecting the reward below board. Thin lines: hand use reversed. Insert: diagram of the brain with sectioned midline structures shaded; optic chiasm, anterior commissure corpus callosum, posterior, habenular and hippocampal commissures. Note the rapid learning of bimanual co-ordination when the animal first began working blind. By the end of the record co-ordination was equally good with or without vision.

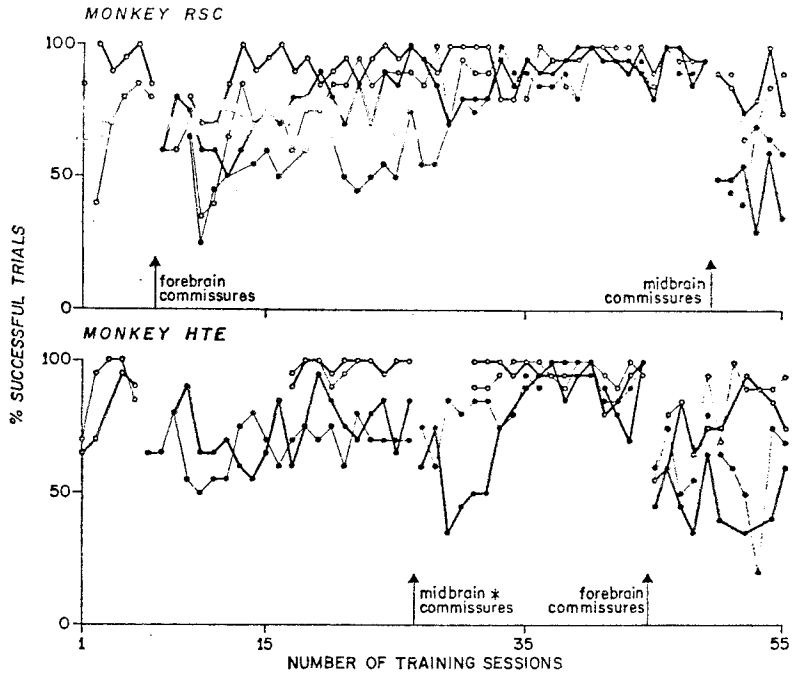


FIG. 3. Co-ordination scores of two monkeys before and after various midline brain lesions. Axes and symbols as in Fig. 2. Section of either forebrain commissures (anterior commissure, hippocampal commissure and corpus callosum) or mid brain commissures (posterior and habenular commissures plus the roof-plate of the midbrain) did not prevent learning of bimanual co-ordination. When both groups of commissures were cut there was a noticeable deficit in blind co-ordination, even when performance under visual control was nearly normal. (* The posterior few millimeters of the corpus callosum were cut at this operation for access to the midbrain commissures).

Results

Four animals began work on the problem in the testing unit shown in Fig. 1. Two were unoperated normal monkeys and two already had partial commissure lesions. All the forebrain commissures had been sectioned in one of these animals; in the other the midline section included all forebrain cross connections and extended posteriorly into the roof plate of the midbrain.

All four first learned to perform the task while watching their hands through open eye-slots. Three learned equally well with either hand combination, but the one animal with the most extensive midline lesion (OPH) would only work with the right hand locating and releasing the reward while the left hand caught it from below. As soon as the animals had

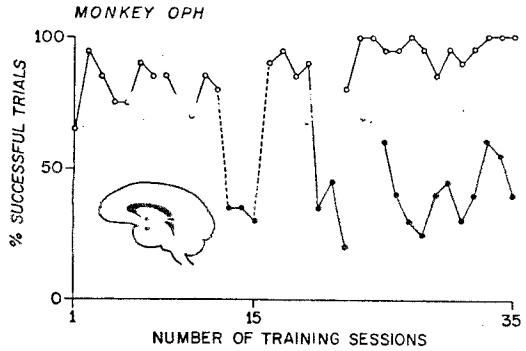


FIG. 4. Co-ordination scores of one monkey (OPH) in which forebrain and midbrain commissures, had been cut before testing began. The right hand was above the board operating the dispenser and the left hand below. Open circles show scores with eyes open, filled circles scores with the cage eye-slots closed. Note the large proportion of errors made when working blind.

become proficient in the task with vision allowed, the forebrain commissures of one of the normal monkeys (RSC) were cut at one operation.

In subsequent training the vision of all the animals was blocked for half of each daily session by closing the eye-slots and various eye-hand combinations were tested daily with and without vision. The first time they began to work blind all four monkeys learned within just a few trials to locate the dispenser by touch with the hand above the board. Initially however they all made large errors in the placement of the lower hand.

Monkey TPS in which the forebrain commissures had been cut before testing began, improved steadily in the placement of the lower hand; and after 12 sessions of blind training, scores with and without vision were not

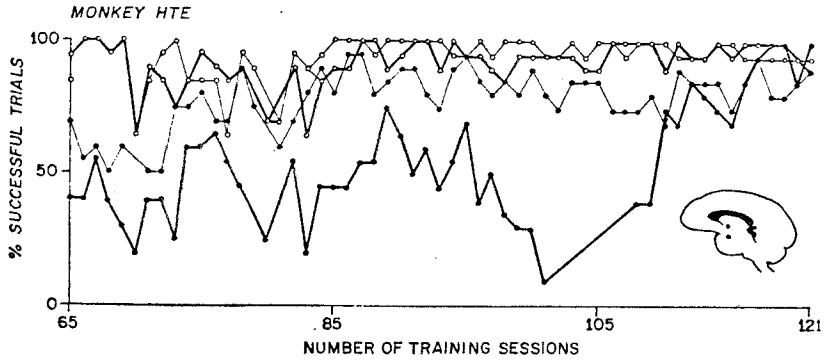


FIG. 5. Co-ordination scores of monkey HTE showing gradual recovery of co-ordination after the double lesions of forebrain and midbrain commissures. Axes and symbols as in Figs. 2–4.

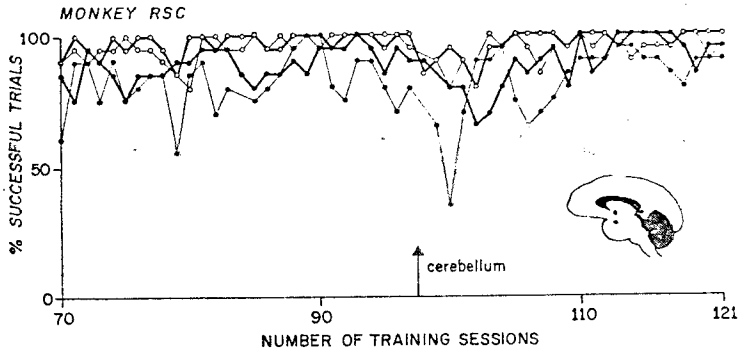
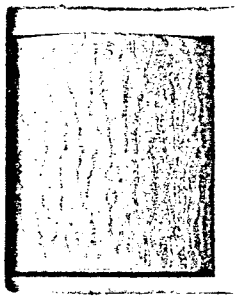


FIG. 6. Co-ordination scores of monkey RSC after recovery from combined section of forebrain and midbrain commissures showing the slight and transient effect of a massive midline lesion of the cerebellum. Axes and symbols as in Figs. 2–5.

appreciably different (Fig. 2). Monkey RSC, in which forebrain commissures were cut after visually guided training was complete, also improved progressively in the accuracy with which the lower hand was located. The improvement was slower than with TPS and reached a comparable level with both hand combinations only after 27 training sessions without vision. In this animal there was also some postoperative falling off in the precision of visually guided movement (Fig. 3), but this became less obvious with further training and was no longer apparent 14 sessions after operation. Monkey HTE which was unoperated at this stage improved with practice, but did not learn to place its lower hand so precisely as either of the first two animals, both of which had no forebrain commissures (Fig. 3). The greatest deficit was shown by the animal (OPH) that had the most extensive midline lesion, section of forebrain commissures plus the roof-plate of the mid-brain. The lower hand was mislocated in the majority of trials and no tendency to improvement was seen after 17 training sessions (Fig. 4). Thus in two monkeys, section of the forebrain commissures, either before or during the learning of this task, did not seem to stop animals from reaching so high a level of performance working blind as they did while their hands were within view. Section of the roof-plate of the midbrain as well as the forebrain commissures produced a marked deficit in coordination when the animal was working blind, whereas performance with vision was as good as that of normal animals.

The possible importance of midbrain cross connections alone was now tested in the monkey HTE, that had already been trained in the problem but had had no surgical intervention. The roof-plate of the midbrain was

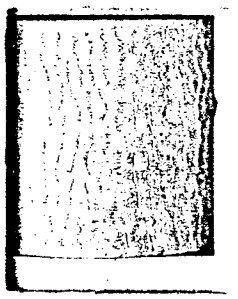
cut leaving the bulk of the forebrain commissures intact. It was necessary during the operation to cut the posterior few millimeters of the corpus callosum for access to the corpora quadrigemina and the posterior commissure and habenula commissure were cut at the same time. In Fig. 2 the scores of this animal tested before and after operation are plotted. Visually guided hand movement was apparently not affected by the operation. Without vision there was a transient reduction in the accuracy of control of the right hand, but within seven training sessions this returned to preoperative levels. Coordination of both hands went on to improve until there was no significant difference in scores with and without vision.



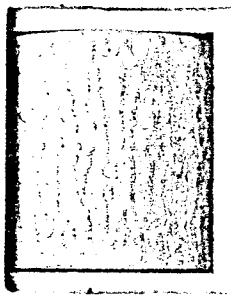
In the two monkeys RSC and HTE further operations were now carried out to produce a combined lesion similar to that of animal OPH. In RSC section of the intercollicular connections and posterior and habenular commissure was added to the previous callosal and anterior commissure lesions. In HTE the dorsal midbrain lesion was extended forward to include the rest of the corpus callosum and the anterior commissure. The result was the same in the two animals (Fig. 3). Both temporarily lost some degree of fine motor control, but, with vision allowed, this cleared up in about five training sessions. The defect in blind coordination was more serious in both animals and persisted with continued misplacement of the lower hand in the test situation. The deficit, in both cases, was like that observed in animal OPH in which a similar large midline lesion had been made before training began.

Over the subsequent months, daily training of both RSC and HTE was continued. Monkey OPH was a very difficult animal to work with in this training apparatus so we did not persist with it. In Fig. 5 the performance of HTE is followed from training session 65 onwards. With the left hand above and right below, blind coordination steadily improved and soon approached that obtained under visual control. With hand use reversed, a defect in coordination remained for several months and then this too disappeared quite suddenly. When training was stopped there was no noticeable impairment of bimanual coordination either in the test situation or in their normal cage life. Similarly in RSC (not illustrated) training over several months steadily improved coordination, and there was no deficit by session 70.

The improvement with long practice, even in animals with double lesions, suggested that yet other crossed pathways might be involvel in bimanual coordination. We checked for the contribution of cerebellar cross connections in monkey RSC with an almost complete midline saggital section of the cerebellum (a small remnant of the anterior lobe escaped damage during surgery). This operation left no symptoms of cerebellar damage in



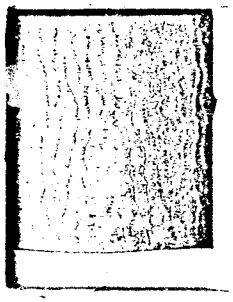
the test performance after the first postoperative week. Figure 6 shows that animal's performance after recovery from section of both intercortical and intercollicular commissures and illustrates that remarkably small and transient effect of the cerebellar lesion on blind or visually guided hand movements. Training of both these animals ceased after 121 sessions (9,000 trials approximately) at which time, in spite of extensive midline surgery. There was no evidence of incoordination between the two hands or of misplacement of the lower hand, with or without visual control.



Since the deficit in bimanual coordination produced by midline lesions could be overcome by extensive practice, it was of interest to know whether the remedial effect of practice came only after brain lesions, or whether bimanual skilled movements tended to become less dependent on constant side-to-side communication in the brain after much repetition. Two animals, (*Macaca speciosa*) RTH and HLD, were used in the same apparatus in an experiment designed to check on this latter possibility. Monkey RTH was trained with and without vision over 32 training sessions until blind coordination was consistently as good as that with visual guidance. Monkey HLD was trained with vision until it had become proficient, but was only allowed three sessions working blind. Nevertheless, during these three sessions it quickly learned to place its lower hand without visual guidance and by the third session the level of performance was equal to that of animal RTH. At this stage both animals underwent simple section of the corpus callosum and anterior commissure. The two animals were tested after allowing 1 week for recovery after operation (see Fig. 7). There was then no difference between them in the accuracy of visually guided movement. Without vision there was a noticeable difference for the first three training sessions during which the monkey (RTH) that had had extensive practice was considerably better than HLD that had not been allowed to practice. Monkey HLD then improved quickly and soon was scoring as well as RTH.

Discussion

Physiological studies (17) as well as behavioral tests (6, 22) indicate that the sensory information needed for sensing the position of the limbs is projected primarily to the contralateral hemisphere. Accordingly, in the test situation successful performance might have been expected to depend heavily on transcallosal exchange between the cortical centers for motor control of the lower arm on one side and those receiving the sensory input from the other arm in the opposite hemisphere. In fact, contrary to these expectations, it proved difficult to demonstrate that bimanual coordination was at all affected by section of the corpus callosum. Added section of midbrain commissures was necessary to produce substantial impairments in the



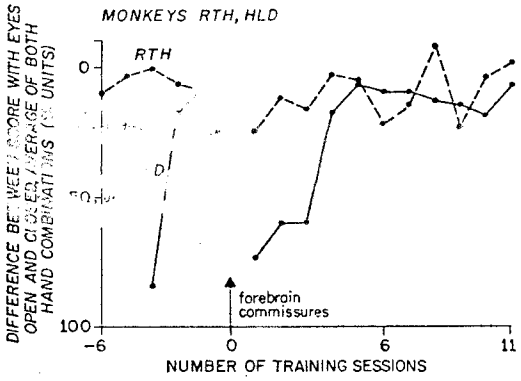


FIG. 7. Co-ordination indices for two monkeys before and after section of the corpus callosum and anterior commissure. Scores for right and left hands working with and without vision were combined as follows:

$$\frac{\text{(Score, eyes open—score eyes closed) for right hand above} + \text{(score eyes open—score eyes closed) for left hand above,}}{2}$$

to give an index which ranges from 0 if there is no difference in performance with and without vision to 100 if all trials with vision are successful and there are no successful trials without vision. The abscissa gives the number of training trials before or after operation. Both animals had been trained with vision for a total of 32 sessions before operation. RTH had worked with and without vision in all sessions, HLD had had only three sessions without vision. Note that after operation the performance of HLD was more affected than that of RTH.

intermanual performance. The predominant finding is that cooperation between the hands is remarkably unimpaired after cutting the forebrain commissures.

This parallels the results of experiments on the visual guidance of hand movement, in which the accuracy of simple reaching after callosal section was the same whether the sensory information was projected to the hemisphere ipsilateral or contralateral to the hand in use (9). An exception was seen in the present experiments, however, where coordination of recently acquired bimanual cooperation was found to be more affected by callosal section than was coordination more firmly stabilized by long practice. The ability to dispense with the corpus callosum appears due in part to functions carried out in the paired centers of the midbrain, a not unexpected finding in view of the importance of midbrain structures in voluntary movement in primates (2).

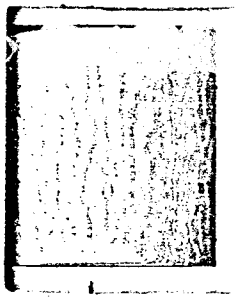
Even with the midbrain commissural pathways sectioned in addition to the forebrain commissures, the slow recovery of coordination and the lack of effect of midline section of the cerebellum show that there must be

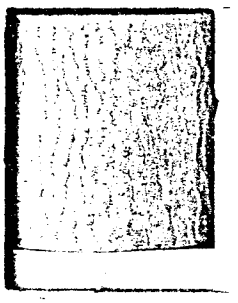
yet other mechanisms for cross coordination. Normal intermanual cooperation may probably be maintained by a number of different neural mechanisms the relative importance of which may vary with the complexity of the task, the relation of this to other concurrent higher nervous functions of perception, choice and learning, and the amount of motor learning already invested in a particular skilled act.

We can see at least four basically different ways by which the bimanual test task in question might be mediated. (*a*) Most obvious is the direct transmission of positional information from one side to the other through the forebrain and midbrain cross connections that were included in the surgery. Interruption of these direct cross-cuing systems led to a partial and largely recoverable disorganization of the target behavior as described above. After elimination of the direct cross connections in forebrain and dorsal midbrain, a variety of additional possible mechanisms for cross integration remain by which the observed gradual recovery of coordination might be explained. (*b*) Sensory target information might be cross-cued centrally through lower-level exchange in uncut spinal and brain-stem systems. Direct ipsilateral sensory projection of somesthesis could play a significant role. The ipsilateral component is reputedly crude for the extremities, but less so for proximal and axial structures. It should be noted that the movements involved in the test task were primarily at the elbow and shoulder rather than in the wrist and digits. The latter are more distinctly lateralized in cerebral representation and their control more profoundly affected by cerebral commissurotomy (*7*, 23).

Mechanisms involving (*c*) less direct cross-cuing through the periphery and through structures bilaterally represented provide further important possibilities. Once the target position is perceived through one hemisphere and the appropriate eye, and the head, neck, trunk, and shoulder girdle adjustments are specified, the target information then becomes automatically mirrored in the opposite hemishpere via the bilateral sensory representation, and perhaps also through central bilateralization of the monitoring for movement intention. With a triangulation on the target thus established bilaterally, it is no problem for the second hemisphere to aim the responding or "catching" hand with high accuracy.

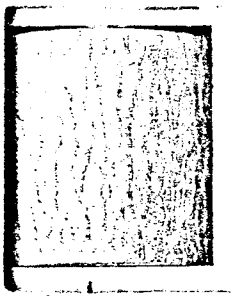
Other possible mechanisms are found in (*d*), the ipsilateral systems for motor control. Direct pathways from the cortex to the spinal cord via the medullary pyramids have an appreciable ipsilateral component (1, 11, 16) and there are also important indirect routes (10, 12, 13). Monkeys in which only ipsilateral, nonpyramidal pathways have been left intact soon develop enough control to perform the role of the catching hand in our test situation (15). There may thus be sufficient ipsilateral motor control, especially with facilitatory support from the main contralateral system re-

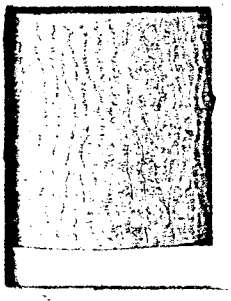




tained intact, to make it unnecessary for the target information to reach the second hemisphere (8). The possibility of some short-circuiting of the main contralateral motor control through undar[illegible]oordinating mechanisms must also be considered (2, 14, 15).

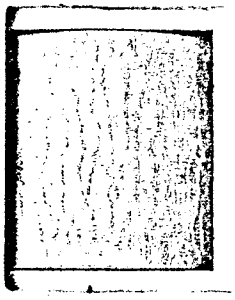
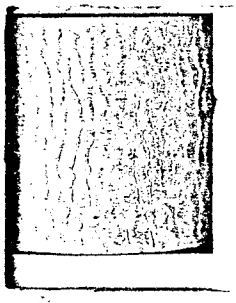
Individually or in combination the fo[illegible]ed mechanisms can readily account for the observed preser[illegible]nual coordination following section of the cerebral commissures. The results point up the importance of these and other possible mechanisms for the bilateral integration of skilled movement under normal conditions.





References

1. BUCY, P. C., and J. F. FULTON. 1933. Ipsilateral representation in the motor and premotor cortex of monkeys. *Brain* **56**: 318–342.
2. DENNY-BROWN, D. 1962. The midbrain and motor integration. *Proc. Roy. Soc. Med.* **55**: 527–538.
3. DOWNER, J. L. DE C. 1959. Changes in visually guided behaviour following mid-sagittal division of optic chiasm and corpus callosum in monkey (Macaca mulatta). *Brain* **82**: 251–259.
4. ETTLINGER, G., and H. B. MORTON. 1963. Callosal section: its effect on performance of a bimanual skill. *Science* **139**: 485–486.
5. GAZZANIGA, M. S. 1966. Visuomotor integration in split-brain monkeys with other cerebral lesions. *Exptl. Neurol.* **16**: 289–298.
6. GAZZANIGA, M. S., and R. W. SPERRY. 1966. Visuomotor control in monkey following brain lesions. *Federation Proc.* **25**: 396.
7. GAZZANIGA, M. S., J. E. BOGEN, and R. W. SPERRY. 1967. Dyspraxia following division of the cerebral commissures. *Arch. Neurol.* **16**: 606–612.
8. GILMAN, S., and D. DENNY-BROWN. 1966. Disorders of movement and behavior following dorsal column lesions. *Brain* **89**: 397–418.
9. HAMILTON, C. R. 1967. Effects of brain bisection on eye-hand coordination in monkeys wearing prisms. *J. Comp. Physiol. Psychol.* **64**: 434–443.
10. KUYPERS, H. G. J. M. 1958. Some projections from the pericentral cortex to the pons and lower brain stem in monkey and chimpanzee. *J. Comp. Neurol.* **110**: 221–225.
11. KUYPERS, H. G. J. M.. 1960. Central cortical projections to motor and somatosensory cell groups. *Brain* **83**: 161–184.
12. KUYPER, H. G. J. M., W. R. FLEMMING, and J. W. FAIRHOLT. 1962. Subcorticospinal projections in the Rhesus monkey. *J. Comp. Neurol.* **118**: 107–137.
13. KUYPERS, H. G. J. M., and D. A. LAWRENCE. 1967. Cortical projections to the red nucleus and the brain stem in the Rhesus monkey. *Brain Res.* **4**, 151–188.
14. LASHLEY, K. S. 1924. Studies of cerebral function in learning: V The retention of motor habits after destruction of the so-called motor areas in primates. *A.M.A. Arch. Neurol. Psychiat.* **12**: 249–273.
15. LAWRENCE, D. G., and H. G. J. M. KUYPERS. 1965. Pyramidal and non-pyramidal pathways in monkeys: anatomical and functional correlation. *Science* **148**: 973–975.
16. LIU, C. N., and W. W. CHAMBERS. 1964. An experimental study of the corticospinal system in the monkey (Macaca mulatta). The spinal pathways and preterminal distribution of degenerating fibers following discrete lesions of

the pre- and post-central gyri and bulbar pyramid. *J. Comp. Neurol.* 123: 257–284.

17. MOUNTCASTLE, V. B., and T. P. S. POWELL. 1959. Central nervous mechanisms subserving position sense and kinesthesis. *Bull. Johns Hopkins Hosp.* 105: 173–200.
18. MYERS, R. E., R. W. SPERRY, and N. M. MCCURDY. 1962. Neural mechanisms in visual guidance of limb movement. *Arch. Neurol.* 7: 195–202.
19. PENFIELD, W. 1954. Mechanisms of voluntary movement. *Brain* [illegible]
20. SCHRIER, A. M., and R. W. SPERRY. 1959. Visuo-motor integration in split-brain cats. *Science* 129: 1275–1276.
21. SPERRY, R. W. 1967. Split-brain approach to learning problems, pp. 714–722. *In* "Neurosciences: A study program," G. C. Quarton, *et al.* [eds.]. Rockefeller University Press, New York.
22. SPERRY, R. W. 1968. Mental unity following surgical disconnection of the cerebral hemispheres. *Harvey Lect. Ser. for 1967.* 62, (in press).
23. SPERRY, R. W., M. S. GAZZANIGA, and J. E. BOGEN. 1968. The neocortical commissures: syndrome of hemisphere deconnection. *In* "Handbook of Clinical Neurology," P. J. Vinken and G. W. Bruyn [eds.]. Vol. 4 (in press). North-Holland Publishing Co., Amsterdam.
24. TREVARTHEN, C. B. 1965. Functional interactions between the central hemispheres of the split-brain monkey, pp. 24–41. *In* "Functions of the Corpus Callosum." E. G. Ettlinger [ed.]. Ciba Foundation Study Group No. 20, J. and A. Churchill Ltd., London.
25. VONEIDA, T. J. 1963. Performance of a visual conditioned response in split-brain cats. *Exptl. Neurol.* 8: 493–504.